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ECOSYSTEM ENGINEERS MODULATE EXOTIC INVASIONS IN RIPARIAN PLANT COMMUNITIES BY MODIFYING HYDROGEOMORPHIC CONNECTIVITY

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ABSTRACT

Patterns of native and exotic plant species richness and cover were examined in relation with ecosystem engineer effects of pioneer vegetation within the Mediterranean gravel bed river Tech, South France. The floristic composition was characterized according to two distinct vegetation types corresponding to two habitats with contrasted conditions: (i) open and exposed alluvial bars dominated by herbaceous communities; and (ii) islands and river margins disconnected from annual hydrogeomorphic disturbances and covered by woody vegetation. A significant positive correlation between exotic and native plant species richness and cover was observed for both vegetation types. However, significant differences in native and exotic species richness and cover were found between these two vegetation types. Higher values of total species richness and Shannon diversity were attained within the herbaceous vegetation type than within the woody type. These differences are most likely related to changes in local exposure to hydrogeomorphic disturbances driven by woody engineer plant species and to vegetation succession. A lower exotic species cover within the woody vegetation type than within the herbaceous type suggested an increase of resistance to invasion by exotic species during the biogeomorphic succession. The engineer effects of woody vegetation through landform construction resulted in a decrease of alpha (α) diversity at the patch scale but, in parallel, caused an increase in gamma (γ) diversity at the scale of the studied river segment. Our study corroborates recent investigations that support the theory of biotic acceptance of exotic species by native species at the local scale (generally $<10\,m^2$) within heterogeneous and disturbed environments. Furthermore, we suggest that in riparian contexts such as the River Tech exotic species trapp sediment at the same time as native species and thus contribute to the increase in ecosystem resistance during the biogeomorphic succession.

KEY WORDS: ecosystem engineer; exotic species; Mediterranean riparian system; species richness; invasibility; hydrogeomorphic disturbance

INTRODUCTION

It has been suggested that biodiversity *per se* could stabilize ecosystem structure and function through space and time by increasing resistance to invasion of exotic species (Hooper and Vitousek, 1998; Hooper *et al*., 2005). In particular, a discussion related to the relationship between native species richness and invasibility of exotic species was earlier initiated in the Elton (1958) biological resistance hypothesis. This hypothesis suggested in contemporary plant ecology that communities with high native species richness are more resistant to invasion of exotic species than communities with low native species richness. Elton's idea was built upon a niche perspective where communities with lower functional diversities are expected to encounter more exotic (in the sense of invasive) species that possess life history traits not found in the resident community. This hypothesis oriented many studies in contemporary ecology, generally testing in terrestrial contexts (e.g. prairie grasslands) whether invasion resistance increases in strongly competitive species-rich communities (Naeem *et al*., 2000; Fridley *et al*., 2007; Souza *et al*., 2011). Elton's hypothesis was supported mostly through controlled experiments and *in situ* field studies under homogeneous natural conditions at plot scales (generally $<10\,m^2$), revealing negative correlations between native and exotic species richness (Levine, 2000; Naeem *et al*., 2000; Kennedy *et al*., 2002).

At local spatial scales and under stable, non-disturbed and homogenous environmental conditions, biotic competitive interactions for gaining access to open space, light, water and nutrients are likely to dominate over all other abiotic and biotic factors, explaining plant assemblages (Kennedy *et al*., 2002; MacDougall *et al*., 2009). However, as noted by Davies *et al*. (2005), spatial heterogeneity in the environment at large scales can lead to the increase of both native and exotic richness. Naeem *et al*. (2000) suggested that, even at the local scale, covarying extrinsic factors such as

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habitat heterogeneity, physical disturbances and soil fertility may decrease the capacity of native diversity to inhibit invasion and in turn modulate exotic–native relationships. Specifically, in the context of riparian environments in which abiotic factors can dominate biotic interactions, Hood and Naiman (2000) came to the same conclusion as Naeem *et al*. (2000). Because of the highly dynamic and disturbed character of riparian systems, these offered a good opportunity to study local effects of extrinsic factors on plant assemblages.

High plant species richness was generally observed within temperate riparian contexts (Tabacchi *et al*., 1996). In theory, as proposed by Elton (1958), the high plant species richness found within riparian contexts and related to hydrogeomorphic disturbances should limit invasibility. Nevertheless, many studies carried out in riparian corridors of the northern temperate zone contradicted Elton's hypothesis by finding positive correlations between exotic and native richness (Hood and Naiman, 2000; Aguiar *et al*., 2006; Chen *et al*., 2010). In light of these findings, riparian plant communities were often described as highly vulnerable to invasion by exotic species mainly as a result of being subjected to hydrogeomorphic disturbances (Moore *et al*., 2001; Tabacchi and Planty-Tabacchi, 2005). For example, DeFerrari and Naiman (1994) observed on rivers of the Olympic Peninsula, WA, USA, that flood frequency and timing represented major controls of plant species richness and the invasibility of riparian zones by exotic plants. The authors noted an increase of both diversity and invasibility in the riparian zone in comparison with adjacent undisturbed upland areas. On the McKenzie River, OR, USA, and the Adour River, South-Western France, Planty-Tabacchi *et al*. (1996) noted the same tendency. Stohlgren *et al*. (1998) showed, in the Central Grasslands of the USA, that riparian areas with hydrogeomorphic instability also favoured plant diversity and invasibility compared with more stable adjacent upland areas. Hood and Naiman (2000) suggested that the three main components associated to the riparian context affecting invasibility are as follows: (i) water flow, controlling diaspore dispersion from sources to new open colonization sites; (ii) flood frequency and magnitude (i.e. the natural flow regime), controlling vegetation recruitment and establishment with reduced competition; and (iii) water availability from the water table, controlling vegetative growth and reproduction.

The potential effect of floods on plant colonization capacity of native and exotic species may vary greatly within the active tract of riparian corridors, depending on the local stability of habitats, on their degree of exposure to hydrogeomorphic fluxes (i.e. water, sediment and nutrient) and on vegetation succession stages (Lonsdale, 1999; Clark and Johnston, 2011). The location along the transversal gradient of hydrogeomorphic connectivity within river corridors and the related patterns of submersion and sediment accumulation are critical in defining plant assemblages and strategies and in modulating biotic interactions (Bendix and Hupp, 2000; Bornette *et al*., 2008). Furthermore, pioneer aquatic and riparian communities do not only respond to hydrogeomorphic disturbances and habitat conditions within the riparian zone but also control fluxes of water (Tabacchi *et al*., 2000), sediment (Gurnell and Petts, 2006), nutrients (Francis *et al*., 2009) and diaspores (O'Hare *et al*., 2012). As a result, within the riparian corridor, many biogeomorphically stabilized pioneer woody vegetation patches emerge during the few years following flood events (e.g. Gurnell *et al*., 2001, 2012; Corenblit *et al*., 2009). These partly hydrogeomorphically disconnected woody vegetation patches clearly contrast with patches of herbaceous vegetation on alluvial bars, which maintain a very high degree of hydrogeomorphic connectivity. Such a dichotomy in hydrogeomorphic connectivity driven by pioneer vegetation acting as ecosystem engineers may directly feed back to community structure and function (Bendix and Hupp, 2000; Corenblit *et al*., 2007).

The aim of the present study was to describe plant species richness and diversity and to correlate exotic and native plant species richness and cover within two contrasted pioneer vegetation types related to two distinct habitats in the active tract of a Mediterranean river: (i) the first habitat was dominated by herbaceous species in the very unstable and hydrogeomorphically highly connected areas, and (ii) the second habitat was 'engineered' (*sensu* Jones *et al*., 1994) and dominated by woody engineer species under rather stabilized and hydrogeomorphically more disconnected areas. Furthermore, it was tested if the resistance of the ecosystem to invasion was higher in less disturbed sites than in highly flood disturbed areas, as suggested by Naeem *et al*. (2000). The feedback dynamics driven by engineer plant species may lead to a modulation of native–exotic interactions. That is, a shift from the dominance of extrinsic hydrogeomorphic processes to the dominance of biotic interactions along the hydrogeomorphic connectivity gradient is expectable. Our hypothesis stated that positive correlations between exotic and native species richness and cover dominated within the vegetation type highly exposed to flood disturbance, whereas negative or an absence of correlation prevailed in the vegetation type less exposed. Such floristic patterns and correlations would suggest that within this river system, the modification of hydrogeomorphic connectivity and ecosystem engineers' activity contributed to the control of native and exotic plant species diversity. A validation of this hypothesis would further underpin that within the riparian context, extrinsic factors remain stronger drivers than competition for determining the exotic species invasibility, as long as the habitat is not fully disconnected from the hydrogeomorphic disturbance regime.

MATERIAL AND METHODS

Study sites

The River Tech, with a channel length of 85 km, is a torrential stream draining a Mediterranean mountainous catchment area of 750 km^2 in the French southeastern Pyrenees (Figure 1). The mean annual discharge is 9.1 $m^3 s^{-1}$ at the river mouth. The River Tech has a contrasted pluvio-nival hydrological regime with two periods of high flows (10–13 $m^3 s^{-1}$) between April and May and between November and January and a low-flow period (4–5 $m^3 s^{-1}$) between July and September. High-magnitude torrential flash floods generally occur in autumn, providing bare substrates for vegetation recruitment in the active tract.

Two study sites near the towns of Céret (site 1) and Le Boulou (site 2) were chosen in the highly dynamic piedmont zone of the River Tech (Figure 1). These two sites correspond to river reaches of approximately 800-m length located 12 km apart from each other. They enclosed an active tract and a riparian margin, referred here together as a riparian corridor, of approximately 100-m width each and having equivalent hydrogeomorphical characteristics, even though local differences existed, mainly in mean channel slope: 0.0033 m m^{-1} for site 1 and 0.0013 m m^{-1} for site 2.

Plant vegetation survey

In 2002, herbaceous and woody pioneer vegetation types were delineated *in situ* on the two sites. The two vegetation types both including different communities were surveyed in summer 2002 through 4-m^2 randomly distributed plots (Figure 2). The total number of plots was $n = 135$: herbaceous type for site 1, $n = 40$; woody type for site 1, $n = 35$; herbaceous type for site 2, $n = 30$; woody type for site 2, $n = 30$. We recorded the ground-projected cover area for each plant species in three strata (understory: 0–1 m, midstory: 1–4 m and overstory: >4 m) within each plot using a 0% to 100% scale for each strata. The cover of each species was cumulative over all three vertical strata. Thus, for a given species, the total absolute cover could be greater than 100%. For native, exotic and total species, we calculated the number and relative abundance (%) of species grouped according to their life span: annual and/or biennial herbs, perennial herbs, shrubs and trees. Then, for each of the two vegetation types and each vegetation group, we calculated total exotic and native species richness, relative proportion of exotic species (%), exotic and native absolute and relative cover (%), Shannon diversity and evenness.

Plant identification was based on the European Flora (Tutin *et al*., 1980; Weber, 1997) and the French Kerguelen's Flora (Kerguelen, 2002). Among the species identified, exotic plant species ('neophytes', *sensu* Pyšek *et al*., 2003) were considered to be introduced after 1500 BP following human activity (Richardson *et al*., 2000; Valéry *et al*., 2008). However, most of the exotic species observed along the River Tech were introduced in Southern France less than 50 years ago (database from Planty-Tabacchi, 1993) with some recent additions such as *Dactyloctenium aegyptium* (L.) and *Bidens subalternans* DC (Tabacchi and Planty-Tabacchi, 2009, unpublished).

Hydrogeomorphic characteristics were estimated at each vegetation type of the two study sites within five plots (total of 10 plots per vegetation type). We characterized the topography of each habitat supporting vegetation types using a

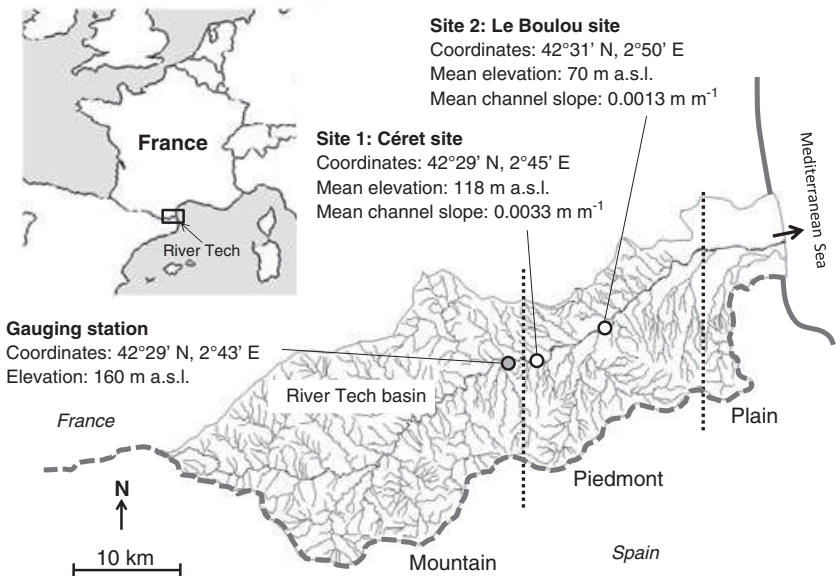

Figure 1. Location of the study area in the Eastern Pyrenees of southeastern France

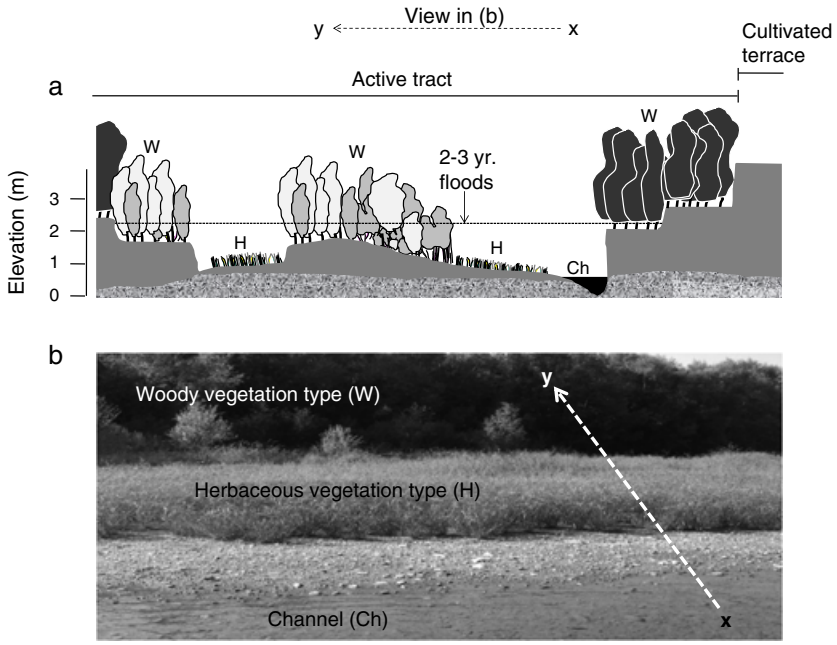

Figure 2. Location of the two vegetation types (herbaceous, H, and woody, W) within the active tract of the River Tech in the piedmont zone. (a) Transverse profile with indicated quasi-annual floods ($T = 2$–3 years). (b) Photographs of the two vegetation physiognomic types taken on site 2 in September 2002. Photographs: D. Corenblit

ZEISS REC ELTA 14™ total station. Surface sediment texture was defined at 100 sample points within the sampling plots using the so-called Wolman method (Wolman, 1954). The large and small particle axes (mm) were measured with a precision calliper. The depth (m) of fine-sediment deposition was determined within plots for each vegetation type using a soil auger. Submersion duration and frequency for each of the two vegetation types were determined using daily discharge data recorded between 1964 and 2004 at the Saint-Paul-sur-Tech gauging station Y0254050, 3 km upstream of site 1 (Figure 1; Table 1).

Data analysis

Statistical differences in hydrogeomorphic parameters between vegetation types were tested using the non-parametric Mann–Whitney *U*-test. Statistical differences in floristic composition between sites and between vegetation types were tested within the exotic and native guilds using two-way analysis of similarity (ANOSIM) with Bray–Curtis similarity (Clarke, 1993). Significance test for ANOSIM was computed by permutation of group membership with 10 000 randomized runs. We used Student's parametric *t*-test to check for statistical differences in the species richness and cover parameters between vegetation types on the two study sites. We used two-way analysis of variance (general linearized model procedure for unbalanced designs) to test for statistical differences on the overall set of data according to the following independent factors: site, vegetation type and site * vegetation type. Data were log-transformed ($\log_{10}[x+1]$) for all comparison tests. All statistical tests were considered significant with a risk alpha of 0.05. We used linear regression models to establish the relationship between exotic and native plant species richness and cover. Regressions were first run for the overall

Table I. Hydrogeomorphic characteristics associated with herbaceous and woody vegetation types within the active tract of the river Tech

Vegetation type (two sites pooled)	Elevation above the summer low-flow level (m)	Fine-sediment subsurface thickness (m)	Submersion duration (number of days per year)	Submersion frequency (number of submersions per year)	Median surface grain size (D_{50} in mm)
Herbaceous					
Mean ± SD	0.48 ± 0.20	0.03 ± 0.20	152.10 ± 121.0	13.70 ± 7.3	12.5 ± 24.3
Woody					
Mean ± SD	1.52 ± 0.30	0.97 ± 0.80	3.00 ± 3.3	3.70 ± 2.7	0.9 ± 0.7

SD, standard deviation
Mann–Whitney *U*-test for comparison between herbaceous (H) and woody (W) types: $p < 0.05$ for all parameters.

dataset and then for each of the two study sites among all sampled plots within the herbaceous and woody types. All statistical analyses were performed with SYSTAT™ v. 11 and PAST v. 2.10.

RESULTS

The habitat dominated by herbaceous vegetation was highly subjected to hydrogeomorphic disturbances, with a mean relative elevation of 0.48 m above the summer low-flow level. The sediment structure consisted generally in a layer of silt and sand of only a few centimetres overlaying the coarse gravel bed deposits. The high variability in submersion duration (error, Table 1) marked a strong gradient from aquatic to semi-terrestrial conditions in the herbaceous type itself. The habitat engineered by pioneer woody vegetation was less exposed to hydrogeomorphic disturbances because of a mean relative elevation of 1.52 m above the low water surface and a significant decrease in submersion duration and frequency. Within the woody-dominated habitat, the sediment structure consisted in a thick (generally >50 cm) fine-sediment layer of silt and sand deposited on the coarse-grained gravel bed.

High species richness and diversity within the riparian active tract

A total of 418 plant species were identified within the River Tech active tract. We observed a very high overall floristic richness and diversity with a mean species richness of $S = 59.4$ per 4 m^2, a mean evenness of $J' = 0.7$ and a mean Shannon's diversity index of $H' = 2.8$ (Table 2). Among the 418 species identified in all plots, 106 were exotic, accounting for approximately 25% of species richness (Appendix 1). Herbaceous plant species accounted for 90% of the sampled species (Table 3). The relative percentage of annual/biennial and perennial herbs was equivalent within the native guild (approximately 45%) whereas short-lived annual/biennial herbs tended to dominate within the exotic guild (54% and 32%, respectively). The relative percentage of shrubs and trees was also equivalent within the native guild (approximately 5%) whereas shrub species dominated within the exotic guild (10% and 4%, respectively). The weight of woody species (mainly shrubs at the juvenile stage) among all life forms was higher in the exotic pool than in the native pool, with 14% and 9% of the sampled species, respectively (Table 3).

Significant variations between vegetation types and between sites

The ANOSIMs indicated that floristic assemblages differed mainly between vegetation types for both the exotic guild ($R = 0.76$, $p < 0.0001$) and the native guilds ($R = 0.80$, $p < 0.0001$). The floristic difference between sites was much less marked for both the exotic and native guilds (with, respectively, $R = 0.19$, $p = 0.0001$; and $R = 0.12$, $p = 0.0009$). S, J' and H' were significantly higher in site 1 ('θ' and 'site' effect in the 'two sites pooled' section of Table 2). These richness and diversity indices were also significantly higher in the herbaceous type than in the woody type at both study sites ('θ' and 'type' effect in the 'two sites pooled' section of Table 2).

Site 1 had more exotic species than site 2 ('†' and 'Ss' effect in the 'two sites pooled' section of Table 2). However, the absolute and relative covers by both native and exotic species did not significantly differ between sites ('•' and 'Ss' effect in the 'two sites pooled' section of Table 2). The highly exposed alluvial bars dominated by the herbaceous vegetation type showed a larger number of both native and exotic species with a more important coverage by exotic species, mainly annual/biennial herbaceous species, compared with the highest topographic levels dominated by the woody type (in 'site 1' and 'site 2' sections on Table 2).

The statistical interactions between site and vegetation type effects ('Ss * T' in the 'two sites pooled' section of the Table 2) were significant for several indices, indicating that the response of species assemblages was variable within the two vegetation types across the two study sites. In particular, the 'Ss * T' effect was significant for both the exotic species relative percentage and relative cover.

Positive correlations and decrease of exotic cover in the woody type

The correlations between exotic and native plant species richness according to herbaceous and woody vegetation types of both study sites pooled together were significantly positive (woody type: $F_{1,\ 64} = 48.0$, $p < 0.0001$; herbaceous type: $F_{1,\ 69} = 143.1$, $p < 0.0001$; Figure 3a; Appendix 2), thus contradicting Elton's (1958) hypothesis. Slopes of linear regression models relating exotic and native plant species richness for the herbaceous and woody vegetation types of both study sites were very similar.

In respect to species cover, the correlations between exotic and native plant species according to herbaceous and woody vegetation were also significantly positive (woody type: $F_{1,\ 64} = 18.4$, $p < 0.001$; herbaceous type: $F_{1,\ 69} = 33.2$, $p < 0.0001$; Figure 3b). However, the slope of the linear regression model for herbaceous type was greater than the one for woody type, indicating that percentage vegetation cover in relation to exotic species was generally higher in the herbaceous type than in the woody vegetation type (Figure 3b). Exotic species cover could reach more than 30% in 44% of the sample plots of the herbaceous type (Figure 3b), whereas it exceeded this value in only one plot in the woody type (Figure 3b). In 29% of the sample plots of the herbaceous type, exotic vegetation cover reaching more than 30% dominated native cover (Figure 3b). However, in only 10% of the sample plots of the herbaceous type did exotic cover largely dominated (>50%) native cover,

Table II. Floristic characteristics for Céret and Le Boulou sites

Parameter	Herbaceous type (mean ± SD)	Woody type (mean ± SD)	Test				Total (mean ± SD)
			Factor	$F_{1,\ 131}$	t	p-value	
Total (two sites pooled)							
Total sp. richness	73.0 ± 35.2	44.7 ± 21.6	Ss	31.6		<0.0001	59.4 ± 32.6
			T	53.1		<0.0001	
			Ss * T	2.8		ns	
Exotic sp. richness	21.4 ± 12.0	12.1 ± 8.5	Ss	48.1		<0.0001	17.0 ± 11.4
			T	49.5		<0.0001	
			Ss * T	7.4		<0.05	
Native sp. richness	51.5 ± 24.7	32.6 ± 15.0	Ss	14.7		<0.0001	42.4 ± 22.6
			T	40.8		<0.0001	
			Ss * T	0.8		ns	
Exotic species (%)	28.9 ± 8.0	25.8 ± 10.1	Ss	22.1		<0.0001	27.4 ± 9.2
			T	7.19		<0.01	
			Ss * T	6.6		<0.05	
Exotic abs. cover (%)	29.2 ± 15.7	17.0 ± 5.1	Ss	0.7		ns	23.3 ± 13.3
			T	23.7		0.0001	
			Ss * T	4.7		ns	
Native abs. cover (%)	30.4 ± 13.1	66.5 ± 19.5	Ss	<0.01		ns	47.8 ± 24.4
			T	156.2		<0.0001	
			Ss * T	9.7		<0.01	
Exotic rel. cover (%)	47.2 ± 11.5	20.9 ± 6.8	Ss	<0.01		ns	34.5 ± 16.2
			T	481.4		<0.0001	
			Ss * T	38.1		<0.0001	
Shannon diversity (H')	3.4 ± 0.7	2.2 ± 0.6	Ss	66.5		<0.0001	2.8 ± 0.9
			T	151.5		<0.0001	
			Ss * T	5.5		<0.05	
Evenness (J')	0.8 ± 0.1	0.6 ± 0.1	Ss	59.8		<0.0001	0.7 ± 0.2
			T	156.0		<0.0001	
			Ss * T	4.0		ns	
Site 1							
Total sp. richnessθ	81.7 ± 39.5	55.3 ± 23.5			3.8	<0.01	69.4 ± 35.4
†Exotic sp. richness	25.1 ± 13.2	16.9 ± 9.0			2.9	<0.01	21.3 ± 12.1
Native sp. richness	56.6 ± 28.2	38.4 ± 17.4			3.7	<0.01	48.1 ± 25.3
†Exotic species (%)	30.6 ± 9.0	30.7 ± 11.4			0.07	ns	30.6 ± 10.1
•Exotic abs. cover (%)	26.1 ± 13.4	17.7 ± 5.1			2.3	<0.05	22.2 ± 11.2
•Native abs. cover (%)	32.9 ± 13.8	66.7 ± 19.5			−7.0	<0.0001	45.9 ± 21.6
•Exotic rel. cover (%)	42.5 ± 10.2	23.4 ± 8.1			68.8	0.0001	33.6 ± 13.3
θShannon diversity (H')	3.6 ± 0.6	2.6 ± 0.5			8.0	<0.0001	3.1 ± 0.8
θEvenness (J')	0.8 ± 0.1	0.7 ± 0.1			9.6	<0.0001	0.8 ± 0.1
Site 2							
θTotal sp. richness	61.3 ± 24.6	32.4 ± 9.3			3.9	<0.0001	46.8 ± 23.5
†Exotic sp. richness	16.6 ± 8.1	6.5 ± 2.1			2.9	<0.01	11.6 ± 7.7
Native sp. richness	44.7 ± 17.2	25.8 ± 7.5			3.7	<0.0001	35.3 ± 16.2
†Exotic species (%)	26.7 ± 5.9	20.2 ± 3.3			0.07	ns	23.4 ± 5.8
•Exotic abs. cover (%)	33.4 ± 17.6	16.1 ± 5.1			2.3	<0.05	24.7 ± 15.5
•Native abs. cover (%)	27.1 ± 11.5	76.4 ± 17.6			−7.0	<0.0001	50.2 ± 27.6
•Exotic rel. cover (%)	53.4 ± 10.0	17.9 ± 2.9			10.4	<0.0001	35.7 ± 19.3
θShannon diversity (H')	3.0 ± 0.8	1.8 ± 0.3			9.0	<0.0001	2.4 ± 0.9
θEvenness (J')	0.7 ± 0.2	0.5 ± 0.1			8.1	<0.0001	0.6 ± 0.2

SD, standard deviation.

Comparison tests were performed on log+1-transformed data. Differences were tested using two-way analysis of variance on the overall observations for testing the effects of study sites (Ss), vegetation types (T) and the combined effect of sites and vegetation types (Ss * T) and t-test for comparison of the two vegetation types for site 1 (Céret) and site 2 (Le Boulou). n total = 135 plots; herbaceous type Céret $n = 40$; woody type Céret $n = 35$; herbaceous type Le Boulou $n = 30$; woody type Le Boulou $n = 30$.

Table III. Total number (S) and percentage of plant species grouped by life span recorded in all plots

Life span	Native (*S*)	Exotic (*S*)	Native (%)	Exotic (%)	Total (*S*)	Total (%)
Annual and biennial herbs	144	57	46	54	201	48
Perennial herbs	143	34	45	32	177	42
Total herbaceous species	287	91	91	86	378	90
Shrubs	17	11	5	10	28	7
Trees	8	4	4	4	12	3
Total woody species	25	15	9	14	40	10
Total	312	106	100	100	418	100

and this was caused by only a few exotic species (Figure 3b; Table 4). A total of 45 species had a cumulative cover of $>1\,m^2$ for the total surface surveyed ($540\,m^2$, i.e., $4\,m^2 * 135$ plots) (Table 4). Among them, 16 were exotic (i.e. 36%). The most abundant herbaceous exotic species (with a total cumulative cover of $>10\,m^2$) were *Cyperus eragrostis* Lam. and *Bidens frondosa* L. The most abundant native herbaceous species were *Echinochloa crus-galli* (L.) P. Beauv. and *Polygonum lapathifolium* L. The most abundant exotic woody species was *Robinia pseudoacacia* L., whereas the most abundant native woody species were *Populus nigra* L., *Alnus glutinosa* L. and *Salix alba* L.

DISCUSSION

The riparian physical environment favours both native and exotic richness

Exotic species represented approximately 25% of all sampled species within the River Tech active tract. Hood and Naiman (2000) noted that comparable proportions of exotic species were observed within several other temperate oceanic or semi-arid riparian corridors subjected to hydrogeomorphic disturbances. For example, DeFerrari and Naiman (1994) showed, within the Dungeness and the Hoh Rivers on the Olympic Peninsula, WA, USA, that exotic plant species accounted for 23% of the sampled species in the two river systems. Planty-Tabacchi *et al.* (1996) measured an exotic proportion of 24% along the Adour River, Southwest France, and 30% along the Lookout Creek, McKenzie River, OR, USA. The authors also reported a proportion of exotic species of 24% and 28% on the Hoh and Dungeness watersheds, respectively.

The positive correlations between exotic and native species richness for both vegetation types clearly indicate that exotic and native species can coexist within one habitat at plot scale when high native species richness prevails. The high native and exotic species richness we observed, in particular within the herbaceous type, indicates that the physical environmental conditions are suitable for both native and exotic species. Lonsdale (1999) and Meiners (2007) pointed out that similar trade-offs in plant life history patterns of native and exotic species can lead to similar population dynamics among native and exotic guilds. Among the native guild of the River Tech, as well as among its exotic guild, more than 85% were generalists or opportunistic (ruderals *sensu* Grime, 2001) species. Such short-lived species have a wide geographical range and currently colonize a variety of riparian habitats in Europe and North America (Shea and Chesson, 2002; Tabacchi and Planty-Tabacchi, 2005). Only a small number of exotic species became largely dominant in a few sample plots located within the herbaceous type at the border of permanently wet channels, mainly *C. eragrostis*, *B. frondosa* and, to a lesser extent, *Paspalum paspalodes* (Michx) Scrib. The niche of these exotic species certainly overlapped the niche of hygrophilous and meso-hygrophilous native species, mainly *E. crus-galli* (L.) P. Beauv., *P. lapathifolium* and *Polygonum hydropiper*

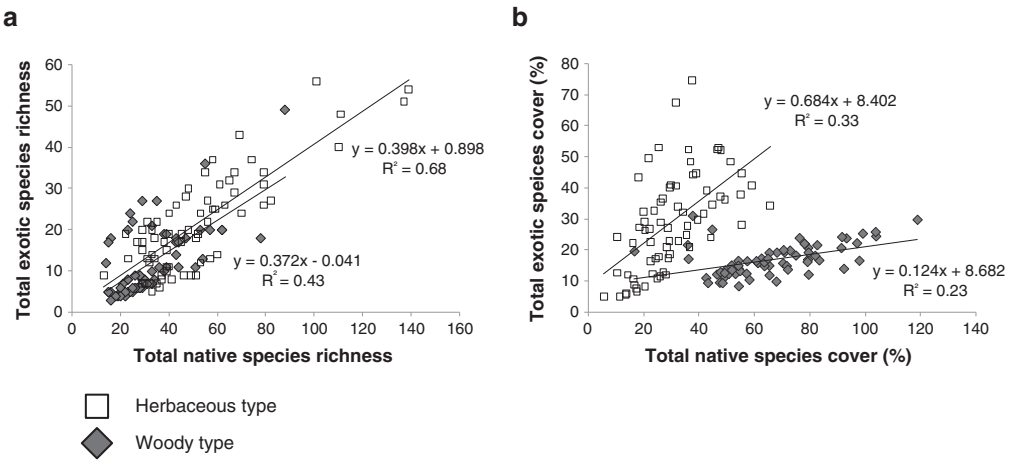

Figure 3. Simple linear regressions between (a) total native and exotic species richness and (b) native and exotic species cover (%) for each vegetation type

Table IV. List of the most abundant native and exotic species sampled within the Céret and Le Boulou study sites

Species with total cover of $>1\,m^2/540\,m^2$	Total m^2 over $540\,m^2$	Mean value (% per $4\,m^2$ plots) ± SD	Type
Populus nigra L.	52.8	9.8 ± 13.9	W
Alnus glutinosa (L.) Gaertner	44.9	8.3 ± 17.3	W
***Cyperus eragrostis* Lam.**	**38.7**	**7.2 ± 11.3**	**H**
Salix alba L. ssp. *alba*	37.0	6.8 ± 12.2	W
***Robinia pseudoacacia* L.**[a]	**15.7**	**2.9 ± 3.8**	**W**
Echinochloa crus-galli (L.) P. Beauv.	15.3	2.8 ± 4.1	H
Rubus caesius L.	14.9	2.8 ± 5.6	W
***Bidens frondosa* L.**	**13.3**	**2.5 ± 4.2**	**H**
Polygonum lapathifolium (L.) Delarbre	11.4	2.1 ± 3.5	H
***Paspalum paspalodes* (Michx) Scribn.**[a]	**9.6**	**1.8 ± 2.8**	**H**
***Arundo donax* L.**	**9.4**	**1.7 ± 3.0**	**W**
***Impatiens balfouri* Hooker fil.**	**7.7**	**1.4 ± 4.5**	**H**
Salix elaeagnos Scop.	6.6	1.2 ± 2.3	W
***Artemisia verlotiorum* Lam.**	**5.9**	**1.1 ± 2.7**	**H**
Salix purpurea L.	5.7	1.1 ± 1.7	W
Typha latifolia L.	4.3	0.8 ± 1.9	H
Rubus ulmifolius Schott	4.1	0.7 ± 1.3	W
***Senecio inaequidens* DC.**	**3.7**	**0.7 ± 2.3**	**H**
Saponaria officinalis L.	3.6	0.7 ± 1.4	H
***Chenopodium ambrosioides* L.**	**3.0**	**0.5 ± 0.8**	**H**
***Xanthium strumarium* L. ssp. *italicum* (Moretti) D. Löve**	**2.9**	**0.5 ± 1.0**	**H**
Brachypodium sylvaticum (Huds.) P. Beauv.	2.8	0.5 ± 0.9	H
Salix fragilis L.	2.7	0.5 ± 0.7	W
Lycopus europaeus L.	2.7	0.5 ± 0.7	H
Chenopodium album L.	2.7	0.5 ± 1.0	H
Polygonum hydropiper (L.) Delarbre	2.6	0.5 ± 0.7	H
***Helianthus rigidus* (Cass.) Desf.**	**2.4**	**0.4 ± 1.4**	**H**
Lythrum salicaria L.	2.03	0.4 ± 0.6	H
***Salix alba* L. ssp. *vitellina* Schüber & Martens**	**1.8**	**0.3 ± 0.8**	**W**
Polygonum persicaria L.	1.8	0.3 ± 0.5	H
***Ludwigia grandiflora* var. *hexapetala* (Hook. & Arn.) Zar., Gu & Raven**	**1.8**	**0.3 ± 0.6**	**H**
Veronica hederifolia L.	1.7	0.3 ± 0.9	H
Artemisia campestris L.	1.6	0.3 ± 0.8	H
Melilotus albus Medik.	1.6	0.3 ± 0.4	H
Piptatherum miliaceum (L.) Cosson	1.5	0.3 ± 1.0	H
Fraxinus angustifolia Vahl.	1.5	0.3 ± 0.9	W
Urtica dioica L.	1.3	0.2 ± 0.6	H
Apium nodiflorum (L.) Lag.	1.3	0.2 ± 0.5	H
***Conyza floribunda* Kunth**	**1.2**	**0.2 ± 0.4**	**H**
Mentha aquatica L.	1.1	0.2 ± 0.4	H
Digitaria sanguinalis (L.) Scop.	1.1	0.2 ± 0.3	H
***Buddleja davidii* Franchet**	**1.1**	**0.2 ± 0.5**	**W**
***Fallopia x bohemica* (Chrtek & Chrtkova) P.J. Bailey**	**1.0**	**0.2 ± 0.5**	**W**
Eupatorium cannabinum L.	1.0	0.2 ± 0.3	H
Dittrichia viscosa (L.) W. Greuter	1.0	0.2 ± 0.3	H

Species with a cumulative cover of $>1\,m^2$ over the total surface surveyed of $540\,m^2$ ($4\,m^2 * 135$ plots) are indicated in the table. Exotic species are indicated in bold and the rest are native species. Vegetation type is indicated (W, woody; H, herbaceous).
[a]Plant species classified as 100 of the most widespread in Europe in the Delivering Alien Invasive Species in Europe database (http://www.europe-aliens.org/index.do).

(L.) Delarbre. However, native species remained dominant within most of the sample plots. We stress that experimental *in situ* investigations will be necessary to determine the factors giving advantage to native species according to the current local hydrogeomorphic conditions.

Thus, at least at the spatiotemporal scale considered in this study, native richness of the herbaceous type does not appear to be affected by exotic species and does not inhibit extensively exotic richness. Because the riparian corridor studied remained sufficiently physically disturbed by floods and thus provided a high resource distribution and habitat reconfiguration, it is most likely that competitive pressure within the active tract remained at rather low levels. Hence, our observations are consistent with the concept of 'biotic

acceptance' under low competition pressure (Stohlgren *et al*., 1999, 2006). Exotic plant species may to some extent be incorporated into hotspots of native plant diversity without causing their immediate disappearance because the native generalists still find adequate local conditions in an unsaturated (i.e. with open space and non-exploited resources) community. The biotic acceptance of plant species observed on the River Tech most likely contributed to the increase of overall plant community species richness, diversity and cover. Therefore, the proportion of exotic species (i.e. richness) may be considered here to represent a net gain of species diversity within the active tract, with corresponding implications in ecosystem functioning. For example, Corenblit *et al*. (2009), who investigated the same study sites on the River Tech, showed the functional importance of sediment trapping by herbaceous mats. According to these findings, exotic richness may potentially represent a gain in the capacity of the herbaceous communities to trap fine sediment and diaspores and to stabilize suitable habitat conditions within the most exposed areas of the active tract.

The notion of invasibility revisited

If it is considered that an 'invaded' environment is one that is clearly dominated in terms of abundance by a few species previously absent (Booth *et al*., 2003). We suggest that in situations such as in our study, the term 'invaded' should rather be replaced by 'absorbent'. The term absorbent would refer to an unsaturated community capable of integrating new plant species, both native and exotic. Indeed, we observed many exotic species (106 on a total of 418) within the riparian corridor, but only one or two very abundant (with a cover of $>50\%$) exotic species in only 5% of the overall sampled plots. In other reaches of the Mediterranean riparian corridors, exotic species invasion can be caused by just one or only a few strong exotic ruderal competitors (e.g. *Fallopia japonica* (Houtt.) Ronse Decraene or *Buddleja davidii* Franchet; see Delivering Alien Invasive Species in Europe database: http://www.europe-aliens.org/index.do), overcoming the destructive effect of hydrogeomorphic disturbances and potentially acting as ecosystem engineers. We suggest that the use of the term 'invasibility' should be restricted to cases with a clear dominance in terms of abundance of one or a few 'aggressive' species.

The statistical significant interactions between site and vegetation type effects (Ss * T in the 'two sites pooled' section of Table 2) for both exotic species' relative proportion and relative cover further suggest that if other river reaches were investigated or if the same reaches would have been investigated at different years, the exotic species' relative proportion and cover could also show differences between vegetation types. Further investigations are needed to understand which combination of factors give advantages to specific species at a given location and period.

Both native and exotic ecosystem engineers modulate resistance to invasion

It was suggested in the literature that in certain cases diversity could positively feed back on species richness, that is, 'the rich get richer', because structurally complex communities may increase microhabitat diversity and thus favour certain invaders (Palmer and Maurer, 1997; Stohlgren *et al*., 2003). This can be the case within ecosystems when communities include ecosystem engineers facilitating the establishment of other species (Bruno, 2000; Bruno *et al*., 2003; Bulleri *et al*., 2008). Within the riparian context, certain assemblages of herbaceous engineer plant species and woody engineer plant species modify habitat conditions at the limit of perennial water channels and on alluvial bars by trapping and stabilizing fine sediment, resources (e.g. nutrients) and huge quantities of both native and exotic diaspores (Tabacchi *et al*., 2005; Gurnell *et al*., 2008). Such ecosystem engineering was observed within the River Tech active tract over a period of three consecutive years from 2003 to 2005 (Corenblit *et al*., 2009). The authors showed that pioneer herbaceous communities, combining exotic and native species, retained during quasi-annual ($T = 2$–3 years) floods fine sediment and diaspores in the active tract near the surface of water bodies. Such processes facilitated inter-annual recruitment of other herbaceous and woody species. The authors also showed that the pioneer woody community trapped huge quantities of sand, thus contributing to the construction of forested topographic levees partly disconnected from hydrogeomorphic disturbances. From the findings by Corenblit *et al*. (2009) and the present results, we suggest the existence of a modification during the biogeomorphic succession in the balance between extrinsic factors (i.e. hydrogeomorphic disturbances) and intrinsic factors (i.e. competition) related to fluvial riparian habitat stabilization and construction driven by engineer species (Figure 4). Such a shift was also identified by Bendix and Hupp (2000) within high-energy streams as a fundamental ecological transition in riparian community assemblage and functioning. The biogeomorphic succession observed on the River Tech simultaneously led to the following: (i) an increase of γ plant diversity (diversity at the scale of the riparian corridor) due to the stabilization and construction of new habitats by pioneer engineering plants; (ii) a local decrease of α plant diversity (diversity of a habitat patch) during the succession related to the exclusion of several native and exotic ruderals, mainly caused by shading of *P. nigra*, *S. alba* and *A. glutinosa* (Corenblit *et al*., 2009); and, as a main contribution of this study, (iii) an increase of resistance to invasion. The increase of resistance to invasion during the biogeomorphic succession was translated, as shown in Figure 3b, by a smaller exotic species cover within the

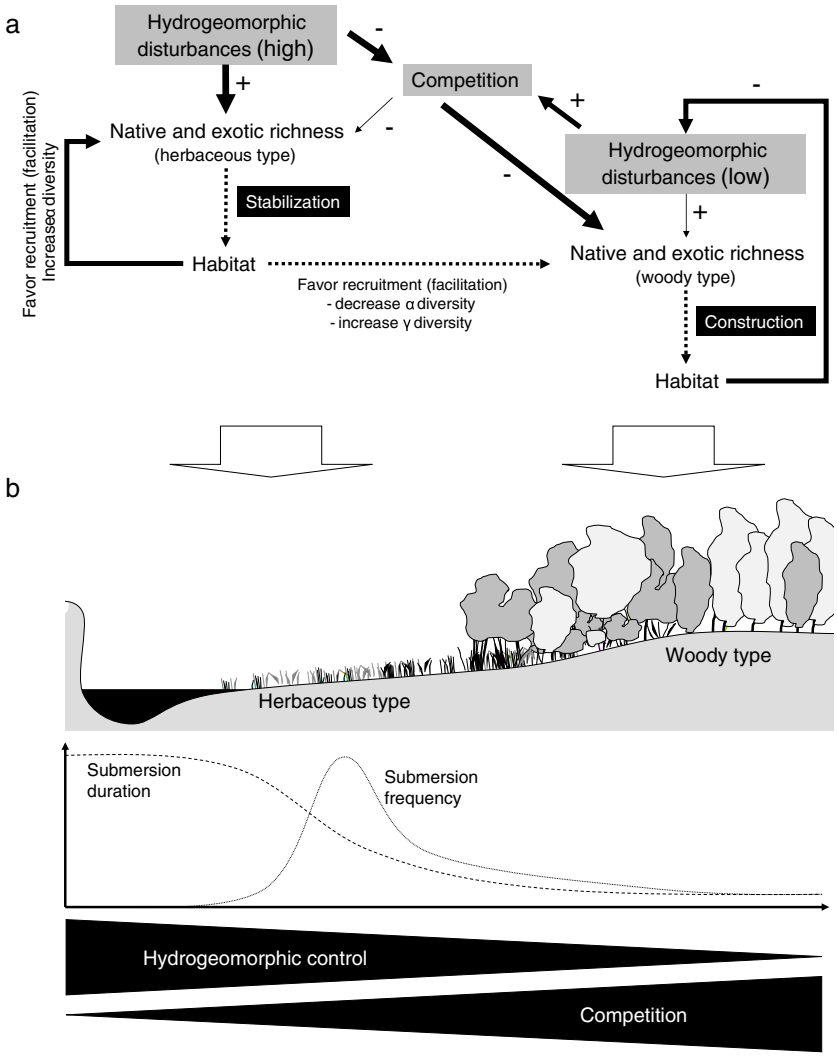

Figure 4. Conceptual model describing (a) how ecosystem engineering by herbaceous and woody pioneer vegetation controls native and exotic richness through the modification of the balance between extrinsic and intrinsic controls, respectively, hydrogeomorphic disturbances and competition and (b) the localization of the processes along the transverse gradient of hydrogeomorphic connectivity. In (a), extrinsic and intrinsic controls are figured in grey boxes and ecosystem engineer effects in black boxes. 'Construction' corresponds to ecosystem engineered *sensu* Jones *et al*. (1994). Increasing or decreasing effects are respectively denoted by + and −. Dotted arrows express processes related to the biogeomorphic succession; solid arrows express primary and secondary controls according to their thickness

woody type in comparison with the herbaceous type. This increase of resistance during the biogeomorphic succession may be related here to the increase of local ecosystem organization in terms of resource exploitation and recycling by prevailing native species (Odum, 1969).

We further suggest that resistance to invasion by one or a few aggressive exotic species could possibly be reinforced within river active tracts by species richness as a whole, that is, encompassing both native and exotic species with redundant or complementary functions. In the current context of the River Tech, the increase of resistance to invasion by aggressive ruderal plant species at the early (herbaceous) stage of the biogeomorphic succession may not be associated to just one or a few native species, but most likely it may be linked to the combined effects of multiple native and exotic ecosystem engineer species forming a functional group enhancing the biogeomorphic succession (Corenblit *et al*., 2009). Therefore, in high-energy Mediterranean riparian ecosystems, exotic species richness may potentially increase resistance to new invasions at the local scale by enhancing and maintaining initial suitable habitat conditions favouring biogeomorphic succession. This will only be the case until woody exotic species with aggressive life history traits succeed in dominating the woody vegetation type, as it was observed by the authors with *B. davidii* Franchet during field visits of upstream reaches of the River Tech. But even

when one invasive woody vegetation type succeeds to dominate, this particular aggressive invader, in turn, could prevent further invasions of other aggressive exotic species and eventually play the functional role of the original native engineer species. This may be the case in particular in the context of anthropogenically altered rivers. For example, *Tamarix* has successfully invaded many rivers in the western USA and replaced in certain reaches native populations of *Populus* and *Salix* (Friedman *et al*., 2005; Stromberg *et al*., 2007). In fact, recent researches in the USA are now questioning the widespread qualification of *Tamarix* as a 'pest plant' and are going even further. Indeed, the ecosystem function role of *Tamarix* replacing Salicaceae species in a human-impacted and hydrogeomorphically altered environment is now considered in the planning of systemic, process-based restoration projects (Stromberg *et al*., 2009).

CONCLUSION

Our findings highlight the importance of hydrogeomorphic disturbance for community assemblage and diversity within riparian corridors and support the theory of a biotic acceptance (Stohlgren *et al*., 2006) within these physically disturbed environments. The positive correlations between native and exotic richness and cover that we observed show that in physically disturbed environments the abiotic factors can act as the most important determinants for both native and exotic plant recruitment and establishment success. These findings suggest that Mediterranean riparian plant communities may incorporate additional exotic species as long as open sites are available and competition remains low within active river tracts. The role of riparian ecosystem engineers in modulating hydrogeomorphic connectivity, and consequently resistance to invasion, during the fluvial biogeomorphic succession was also highlighted. We thus agree with Hood and Naiman (2000) and Naeem *et al*. (2000) who pointed out that Elton's resistance hypothesis may be valid in many cases but that resistance to invasion according to competition may be modulated by the degree of exposure to hydrogeomorphic disturbances. In turn, the hydrogeomorphic connectivity within riparian corridors is ultimately controlled by engineer plant species, both native and exotic, modulating the geomorphic habitat template.

From our observations and findings and in accordance with the suggestion by Stromberg *et al*. (2009), we propose that, under certain conditions, the colonization by exotic species of bare habitat within riparian corridors could represent an opportunity for the conservation or restoration of plant diversity and fundamental ecological functions in river systems, such as sediment, nutrient, organic matter and diaspore retention. Today, in the context of global environmental change (e.g. global warming), the examination of ecological functions of any potential future engineer species on 'novel ecosystems' (*sensu* Hobbs *et al*., 2006), independently from their geographical origin, is needed to fully understand river ecosystem functioning and to find the best solutions for sustainable river management practices.

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APPENDIX 1

LIST OF EXOTIC SPECIES IDENTIFIED IN JUNE AND SEPTEMBER 2002 ON THE SITES OF CÉRET AND LE BOULOU. RELATIVE FREQUENCY PER PLOTS, LIFE SPAN AND STATUS ARE INDICATED. LIFE SPAN: A/B = HERBACEOUS ANNUAL AND/OR BIENNIAL SPECIES, P = HERBACEOUS PERENNIAL, S = SHRUBS, T = TREES. STATUS: N = NATURALIZED, I = INVASIVE.

Exotic species	Herbaceous type relative freq. (%)	Woody type relative freq. (%)	Life span	Status
Abutilon theophrasti Medik.	<0.01	0	a/b	N
Acacia dealbata Link	0.08	0.69	s	I
Acacia retinodes Schltdl.	0	<0.01	s	N
Agave americana L.	<0.01	0	p	I
Alcea rosea L.	<0.01	<0.01	a/b	N
Amaranthus albus L.	<0.01	0	a/b	N
Amaranthus blitoides S. Wats.	0.06	0	a/b	N
Amaranthus blitum L.	<0.01	0	a/b	N
Amaranthus caudatus L.	<0.01	0	a/b	N
Amaranthus cruentus L.	0	0.02	a/b	N
Amaranthus deflexus L.	0.09	0.02	a/b	N
Amaranthus hybridus L.	0.05	0	a/b	N
Amaranthus retroflexus L.	0.16	0.04	a/b	N (I)
Anagallis monelli L.	<0.01	0	a/b	N
Artemisia verlotiorum Lam.	**5.68**	**2.90**	a/b	I
Arundo donax L.	0.73	**20.09**	s	I
Aster salignus Willd	<0.01	<0.01	p	I
Aster squamatus (Spreng.) Hieron.	0.02	0	a/b	N (I)
Atriplex tatarica L.	0.03	0.43	a/b	N
Bidens frondosa L.	**16.22**	0.09	a/b	I
Bidens subalternans L.	0.01	<0.01	a/b	N
Boussingaultia baselloides Kunth	0	<0.01	p	N (I)
Brassica napus L. ssp. *rapa*	<0.01	<0.01	a/b	N
Bromus wildenowii Kunth	<0.01	<0.01	p	I
Buddleja davidii Franch.	0.64	**1.22**	s	I
Calendula officinalis L.	<0.01	0	a/b	N
Chenopodium ambrosioides L.	**3.61**	0.02	a/b	N
Citrullus colocynthis (L.) Schrad.	<0.01	<0.01	a/b	N
Citrullus lanatus (Thunb.) Matsum. & Nakai	<0.01	0	a/b	N
Conyza blakei (Cabrera) Cabrera	0.39	<0.01	a/b	N (I)
Conyza bonariensis (L.) Cronq.	0.96	0.40	a/b	I
Conyza canadensis (L.) Cronq.	0.04	<0.01	a/b	I
Conyza floribunda Kunth	**1.26**	0.37	a/b	N (I)
Conyza sumatrensis (Retz.) E. Walker	0.22	0.03	a/b	I
Coronopus didymus (L.) Sm.	0.02	0	a/b	N
Cortaderia selloana (Schultes) Asch. & Graebn.	<0.01	0.42	p	I
Cucumis melo L. var. *cantalupensis*	<0.01	0	a/b	N
Cucumis melo L. var. *inodorus*	<0.01	0	a/b	N
Cucurbita maxima Duchesne	<0.01	<0.01	a/b	N
Cucurbita moschata (Duch. ex Lam.) Duch. ex Poir.	<0.01	0	a/b	N
Cyperus eragrostis Lam.	**46.35**	**1.75**	p	I
Cyperus rotundus L.	<0.01	0	p	I
Datura inoxia P. Mill.	<0.01	0	a/b	N
Datura stramonium L.	0.29	0.04	a/b	I
Echinochloa colona (L.) Link	0.02	0	a/b	N (I)
Eleusine indica (L.) Gaertn.	<0.01	0	a/b	N (I)
Eragrostis mexicana (Hornem.) Link	0.01	0	a/b	N
Erigeron annuus (L.) Pers.	0.21	<0.01	a/b	I
Escholtzia californica Cham.	<0.01	<0.01	a/b	N
Euphorbia maculata L.	<0.01	0	a/b	N (I)

Bolded data indicates relative % > 1 ; underlinded data indicates relative% > 10.

Appendix 1. (Continued)

Exotic species	Herbaceous type relative freq. (%)	Woody type relative freq. (%)	Life span	Status
Fallopia japonica (Houtt.) Ronse Decr.	0.01	0.11	s	I
Fallopia x bohemica (Chrtek & Chrtkova) J.P. Bailey	0	**2.30**	s	I
Ficus carica L.	0.01	0.01	s	N
Galinsoga quadriradiata Ruiz & Pav.	0.03	0	a/b	N
Glyceria striata (Lam.) Hitchc.	0.03	0	p	N
Helianthus rigidus (Cass.) Desf.	0.10	5.21	p	I
Heliotropium currasavicum L.	<0.01	0	p	N
Impatiens balfouri Hooker fil.	<0.01	**17.53**	a/b	I
Impatiens glandulifera Royle	<0.01	0.12	a/b	I
Iris germanica L.	<0.01	<0.01	p	N
Juglans regia L.	0	<0.01	t	N
Laurus nobilis L.	0	0.08	s	I
Lepidium virginicum L.	0.01	0	a/b	N
Lolium multiflorum Lam.	<0.01	0	p	N
Lonicera japonica Thunb.	0	0.13	s	I
Ludwigia grandiflora var. *hexapetala* (Hook. & Arn.) Zar., Gu & Raven	**2.16**	0	p	I
Lychnis coronaria (L.) Desr.	<0.01	0	p	N
Lycopersicon esculentum Mill.	0.14	<0.01	a/b	N
Narcissus x incomparabilis Mill.	0	<0.01	p	N
Nicotiana glauca Graham	<0.01	<0.01	s	I
Oenothera biennis L.	0.05	<0.01	a/b	N
Oenothera parviflora L.	<0.01	0	a/b	N
Oenothera suaveolens Desf. ex Pers.	<0.01	<0.01	a/b	N
Opuntia stricta (Haw.) Haw.	<0.01	0	p	I
Oxalis corniculata var. *purpurea* Parl.	<0.01	0	a/b	N
Oxalis corymbosa (DC.) Lourteig	0	<0.01	p	N
Oxalis europaea Jord.	<0.01	0	p	N
Oxalis latifolia Kunth	0	<0.01	p	N (I)
Oxalis purpurea L.	<0.01	0	p	N
Panicum capillare L.	**1.00**	<0.01	a/b	N
Panicum dichotomiflorum Michx.	0.54	0	a/b	N
Papaver somniferum L.	<0.01	0	a/b	N
Parthenocissus inserta (A. Kern.) Fritsch	0	0.29	s	I
Paspalum paspalodes (Michx) Scribn.	**11.77**	<0.01	p	I
Populus deltoides Bartr. ex Marsh.	0	**1.11**	t	N
Prunus domestica L.	0	0.06	s	N
Prunus persica (L.) Batsch	<0.01	<0.01	s	N
Robinia pseudoacacia L.	**1.87**	**32.17**	t	I
Salix alba ssp. *vitellina* (L.) Schüb. & Mar.	0.10	**4.01**	s	N
Salpichroa origanifolia (Lam.) Baill.	<0.01	<0.01	p	I
Senecio inaequidens DC.	**1.51**	**5.61**	p	I
Setaria geniculata Beauv.	0.04	<0.01	p	N
Setaria italica (L.) Beauv.	<0.01	0	a/b	N
Setaria pumila (Poir.) Roemer & Schultes	<0.01	0	a/b	N
Silene chalcedonica (Linnaeus) Krause	<0.01	0	p	N
Solanum chenopodioides Lam.	<0.01	<0.01	p	N (I)
Solanum sarrachoides Sendtn.	0.18	<0.01	a/b	N
Sorghum halepense (L.) Pers.	0.32	0.35	p	I
Sporobolus indicus (L.) R. Br.	0.03	<0.01	p	I
Trachycarpus fortunei (Hook.) Wendl.	0	0.14	t	N
Verbena venosa Gillies & Hook.	<0.01	0	a/b	N
Veronica persica Poir.	0.51	<0.01	a/b	N
Vitis vinifera L. ssp. *vinifera*	0	0.12	s	N
Xanthium spinosum L.	0.01	0	a/b	N
Xanthium strumarium L. ssp. *italicum*	**2.42**	**2.06**	a/b	I
Yucca gloriosa L.	0	0.02	s	I

APPENDIX 2

CÉRET SITE (TOP): SIMPLE LINEAR REGRESSIONS BETWEEN WOODY NATIVE AND EXOTIC SPECIES RICHNESS; ANALYSIS OF VARIANCE (A) FOR WOODY TYPE: $F_{1,\ 34} = 13.9$, $P < 0.001$; (B) FOR HERBACEOUS TYPE: $F_{1,\ 39} = 65.5$, $P < 0.0001$; WOODY NATIVE AND EXOTIC SPECIES COVER (%); ANALYSIS OF VARIANCE FOR (C) WOODY TYPE: $F_{1,\ 34} = 5.9$, $P < 0.05$; (D) FOR HERBACEOUS TYPE: $F_{1,\ 39} = 30.7$, $P < 0.0001$. LE BOULOU SITE (DOWN): SIMPLE LINEAR REGRESSIONS BETWEEN WOODY NATIVE AND EXOTIC SPECIES RICHNESS; ANALYSIS OF VARIANCE FOR (A) WOODY TYPE: $F_{1,\ 29} = 53.8$, $P < 0.0001$; (B) FOR HERBACEOUS TYPE: $F_{1,\ 29} = 92.2$, $P < 0.0001$; WOODY NATIVE AND EXOTIC SPECIES COVER (%); ANALYSIS OF VARIANCE (C) FOR WOODY TYPE: $F_{1,\ 29} = 46.2$, $P < 0.0001$; (D) FOR HERBACEOUS TYPE: $F_{1,\ 29} = 24.2$, $P < 0.0001$.